A STUDY OF THE MECHANISM INVOLVED IN SHIFTING OF THE PHASES OF THE ENDOGENOUS DAILY RHYTHM BY LIGHT STIMULI

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A persistent diurnal rhythm of color change in the fiddler crab, Uca, was first reported by Abramowitz in 1937, and has been abundantly confirmed by numerous investigators since that time. The character of the chromatophore rhythm is such that the crabs darken by day and blanch by night owing to dispersion and concentration, respectively, of the melanin within their melanophores. This rhythm has been discussed most recently and described in considerable detail by Brown, Fingerman, Sandeen and Webb (1953). These investigators demonstrated that the rhythm not only persists for long periods in constant darkness, but actually increases in amplitude to reach a maximum value only after ten days to two weeks. This high value was then observed to persist without diminution for the longest period of observation which was about a month. Furthermore, there appeared to be no measurable drift of the rhythm away from its normal phase relations with solar day-night, indicating the mechanism to have a remarkable precision of frequency determination. This frequency was shown by Brown and Webb (1948) to be independent of temperature over the twenty degree range from 6 to 26° C.

Although the mechanism appears to be a moderately stable one in the fiddler crab, it was shown by Brown and Webb (1949), Webb (1950), and Brown, Fingerman, Sandeen and Webb (1953) to be capable of having its phases readily shifted by light-to-dark and dark-to-light changes under certain circumstances. Examples of these shifts are (1) a backward shift of 4 to 5 hours in the phases of the rhythm by three consecutive midnight-to-6 A.M. periods of illumination of animals otherwise in continuous darkness, (2) a forward shift of about 6 hours in animals whose rhythm had been inhibited by several days sojourn in continuous bright illumination and then were placed in constant darkness at 7 A.M., and (3) a shift of about twelve hours, or in other words a reversal, of phases by a few cycles of illumination from 7 P.M. to 7 A.M. and darkness from 7 A.M. to 7 P.M. Brown and Webb (1949) using illuminations of 150, 80, and 50 ft. c. found that the brighter the light the sooner the reversal. With the highest illumination, reversal occurred on the first day and with 40 ft. c. it occurred on the fourth. Once shifted, the rhythms are as stable in their new phase relations as they were in their original normal ones.

The experiments to be described were performed in order to gain further insight into the mechanism involved in inducing persistent shifts and certain other modifications in the endogenous diurnal rhythm.

Materials and Methods

For the experiments to be described, 400 fiddler crabs were collected at Chapoquoit, near Woods Hole, Massachusetts at about three o'clock on the afternoon of June 24, 1952. They were kept in the natural daylight of the laboratory until 7:00 p.m. when they were divided into sixteen groups of 25 crabs each and placed in white enamelled pans in sea water to a depth of about a centimeter. One group, the control one, whose normal rhythm was to be determined was placed in darkness and left for the duration of the experiment. The remaining fifteen groups, the experimental ones, were placed in the conditions of illumination to which they were to be exposed during the night (7 p.m. to 7 a.m.) and the next morning placed in the lower illumination or darkness to which they were to be exposed by day (7 a.m. to 7 p.m.).

The illuminations for the experiments were obtained by frosted incandescent lamps of various wattages held at different distances above the white pans containing the animals. The illuminations were measured with a Weston photometer. The nighttime-daytime illuminations for the fifteen groups of animals subjected to the alternating illuminations were, in ft. candles, respectively: (1) 100–80, (2) 100–50, (3) 100–10, (4) 100–2, (5) 100–0, (6) 50–10, (7) 50–5, (8) 50–2, (9) 25–10, (10) 25–5, (11) 25–2, (12) 10–5, (13) 10–2, (14) 5–2, (15) 2–0.

The temperatures in the inside rooms of the Marine Biological Laboratory in which the experiments were carried on did not show any significant diurnal variation, and there was an irregular variation of only three or four degrees at most during the course of the eleven days in which the experiment was carried out. All the animals, furthermore, both experimentals and controls, were subjected to essentially the same temperature conditions other than the rhythmic differences in heat radiation during the periods of illumination.

The experimental groups were subjected to the twelve-hour alternating conditions of illumination for six days; at 7 p.m. on June 30, they were placed in constant darkness. Beginning at 11 p.m. and continuing at six-hour intervals (11 p.m., 5 a.m., 11 a.m., 5 p.m., ...) for four daily cycles the average chromatophore stage of ten crabs randomly sampled from the fifteen experimental groups and the controls were staged by the method of Hogben and Slome (1931). Through the next or fifth daily cycle the chromatophores were staged at hourly intervals.

Experiments and Results

A summary of the results is found in Table I.

1. *Controls:* The control group possessed a high-amplitude rhythm at the time the staging of chromatophores commenced and showed no significant increase during the five-day period of study. The highest value was found at 11 a.m., and the lowest at 11 p.m. in every daily cycle.

2. *100–80 ft. c.:* In these, it is evident that there was a strong initial depression of rhythm-amplitude, which rapidly diminished during the five days. In every cycle the maximum stage was now at 5 a.m. and the minimum at 5 p.m.

3. *100–50 ft. c.:* This group, unlike the preceding, exhibited little or no initial amplitude depression nor increase during the period of observation. It resembled the preceding in having the maximum average stage always at 5 a.m. and the minimum at 5 p.m.

TABLE I

The average stage of melanin dispersion at each of four times of day, under constant conditions, for Uca which were earlier subjected to five days of higher illumination by night and lower illumination by day

Illum. (ft. c.)	11 P.M.	5 A.M.	11 A.M.	5 P.M.	Illum. (ft. c.)	11 P.M.	5 A.M.	11 A.M.	5 P.M.
Control	1.0†	2.3	5.0*	3.8	50–2	2.7*	1.0†	1.6	1.8
	1.0†	1.9	4.7*	4.1		2.8*	1.4	1.0†	1.6
	1.2†	1.9	4.5*	3.5		3.4*	1.3†	1.9	2.8
	1.1†	2.4	4.7*	4.4		3.0*	1.1†	1.9	2.4
	1.3†	3.1	4.5*	3.5		4.0*	1.4†	1.9	3.9
100–80	1.3	1.8*	1.3	1.0†	25–10	1.1†	1.9*	1.8	1.6
	1.2	1.2*	1.0	1.0†		1.0†	2.0*	1.7	1.3
	1.3	3.6*	2.9	1.1†		1.2†	3.2*	3.2	2.3
	1.9	4.3*	3.0	1.1†		1.6†	3.2	4.2*	1.7
	2.3	4.0*	2.3	1.0†		1.3†	3.7*	2.7	1.7
100–50	3.4	4.7*	2.2	1.2†	25–5	1.2†	1.3	2.2	2.4*
	2.4	4.2*	1.7	1.2†		2.3	2.1†	2.1	2.5*
	3.4	4.2*	3.5	1.1†		2.2†	2.9	3.9*	3.2
	3.0	4.5*	2.7	1.2†		2.4†	3.1	4.0	4.0*
	3.4	3.8*	3.1	1.4†		1.8†	2.9	2.8	3.5*
100–10	3.5*	3.0	1.6	1.0†	25–2	1.3	1.0†	1.2	1.3*
	1.8	3.0*	1.4	1.0†		1.3	1.0†	1.3	1.3*
	2.8	3.6*	2.7	1.2†		1.4	1.0†	2.0	2.6*
	2.5	3.1*	1.6	1.0†		2.6	1.0†	2.6	3.7*
	2.5	3.2*	1.7	1.1†		2.6	1.0†	1.3	2.9*
100–2	1.8*	1.3	1.0†	1.4	10–5	1.2	1.1†	1.5	2.0*
	1.7*	1.0	1.0†	1.0		1.3†	1.3	2.2*	1.8
	1.9	1.6†	2.0	2.7*		1.2†	2.0	3.4	3.6*
	2.7	2.3	2.1†	3.0*		1.7†	1.7	3.0	3.3*
	3.0	2.1	2.0†	3.2*		1.0†	2.4	3.0*	2.7
100–0	4.4*	3.8	1.0†	3.2	10–2	1.6	1.3†	1.9	2.1*
	3.9*	3.0	1.0†	1.9		1.0†	1.4	1.6*	1.4
	4.4*	1.7	1.0†	2.4		1.7†	2.1	2.3	2.9*
	3.8*	2.1	1.0†	2.5		2.4	1.9†	3.1*	2.7
	4.0*	2.7	1.0†	3.0		2.5	1.7†	1.7	3.0*
50–10	2.1	3.9*	2.4	1.2†	5–2	1.0†	1.2	2.1	2.3*
	2.1	4.4*	3.2	1.2†		1.1†	1.8	2.7*	2.1
	1.9	4.9*	4.7	1.5†		1.1†	1.5	3.0*	2.6
	1.5	4.3*	3.6	1.2†		1.0†	1.0	4.0*	2.2
	2.4	4.6*	3.6	1.5†		1.2†	1.6	2.6*	2.5
50–5	1.9*	1.8†	1.7	1.6	2–0	2.4	1.2†	2.8	2.9*
	1.6	1.4†	1.4	1.8*		2.0	1.3†	2.9	3.4*
	1.3†	1.8	2.6*	2.2		3.1	1.7†	3.7	4.0*
	2.3	1.8†	2.7*	2.6		3.2	1.4†	3.7	4.5*
	2.6	1.9†	3.0*	2.4		2.6	1.5†	2.5	3.4*

* Signifies maximum values for a cycle.
† Signifies minimum values for a cycle.

4. *100–10 ft. c.:* The group subjected to these illuminations appeared to show an intermediate degree of depression in amplitude from the beginning and no systematic increase thereafter; but still again, the maximum was nearly always at 5 A.M. and the minimum always at 5 P.M.

5. *100–2 ft. c.:* This group showed initial amplitude depression with a rapid increase during the five days in darkness. Now, the maximum evidently was between 5 and 11 P.M. and the minimum between 5 and 11 A.M.

6. *100–0 ft. c.:* This was the only one of the experimental groups which had undergone a complete reversal of phases. The amplitude was very great from the start and showed no increase. The maximum pigment dispersion was seen at 11 P.M. and the minimum at 11 A.M. in every cycle.

7. *50–10 ft. c.:* This group showed little or no initial depression of amplitude. The maximum occurred at 5 A.M. and the minimum at 5 P.M. in every instance.

8. *50–5 ft. c.:* This group initially showed not only great depression in rhythm amplitude, but initially almost an absence of a recognizable daily cycle. A clear daily cycle did reappear in two or three days and gain in amplitude. But now, strangely, the maximum was close to or at 11 A.M. and the minimum at 5 A.M.

9. *50–2 ft. c.:* This group also showed an initial low amplitude of rhythm, but one which increased rapidly. The maximum value was at 11 P.M. in every cycle and the minimum at 5 A.M. in all but one.

10. *25–10 ft. c.:* An initial amplitude depression was observed in this group but it rapidly disappeared. The time of maximum dispersion appeared to lie between 5 and 11 A.M. and the minimum was always at 11 P.M.

11. *25–5 ft. c.:* The rhythm of this group exhibited an initial depression, and the maximum was between 11 A.M. and 5 P.M. with the minimum at 11 P.M. in four out of the five cycles.

12. *25–2 ft. c.:* In this group, there was an initial depression in amplitude which rapidly vanished; the daily cycle was reasonably symmetrical with an unequivocal maximum at 5 P.M. and minimum at 5 A.M.

13. *10–5 ft. c.:* A great reduction in rhythm amplitude was initially seen in this group. The time of maximum pigment dispersion appeared clearly to lie between 11 A.M. and 5 P.M., and the minimum close to 11 P.M.

14. *10–2 ft. c.:* Again, the amplitude gradually increased during the five days in darkness. The time of the maximum was sometimes seen at 11 A.M. and sometimes at 5 P.M. The minimum, on the other hand was distributed between 11 P.M. and 5 A.M. during the five daily cycles.

15. *5–2 ft. c.:* The amplitude for this group was rather low throughout the five days. The minimum was invariably at 11 P.M. and the maximum nearly always at 11 A.M.

16. *2–0 ft. c.:* There was only slight, rapidly transitory amplitude depression in this group. The maximum value was clearly at 5 P.M. and the minimum at 5 A.M.

Discussion and Conclusions

Viewing the data of Table I as a whole, it is clearly evident that even though the animals have all received in common a higher illumination during 12 hours from 7 P.M. to 7 A.M. and a lower one from 7 A.M. to 7 P.M., there is to be found among the results a whole spectrum of apparent kinds and degrees of shifts of the phases

of the daily rhythm. Furthermore, for any given illumination combination, although the amplitude of the rhythm might undergo considerable change during the five-day period of observation after the animals were left in darkness, the phases of the rhythm in no case showed any evidence of a drift in one direction or the other. The forms of the daily variations of Table I were essentially confirmed on the last day of the five-day series when staging of chromatophores was performed hourly.

In order to obtain a better estimate of the direction and amount of shift in the times of the phases of the rhythms in the experimental crabs away from the con-
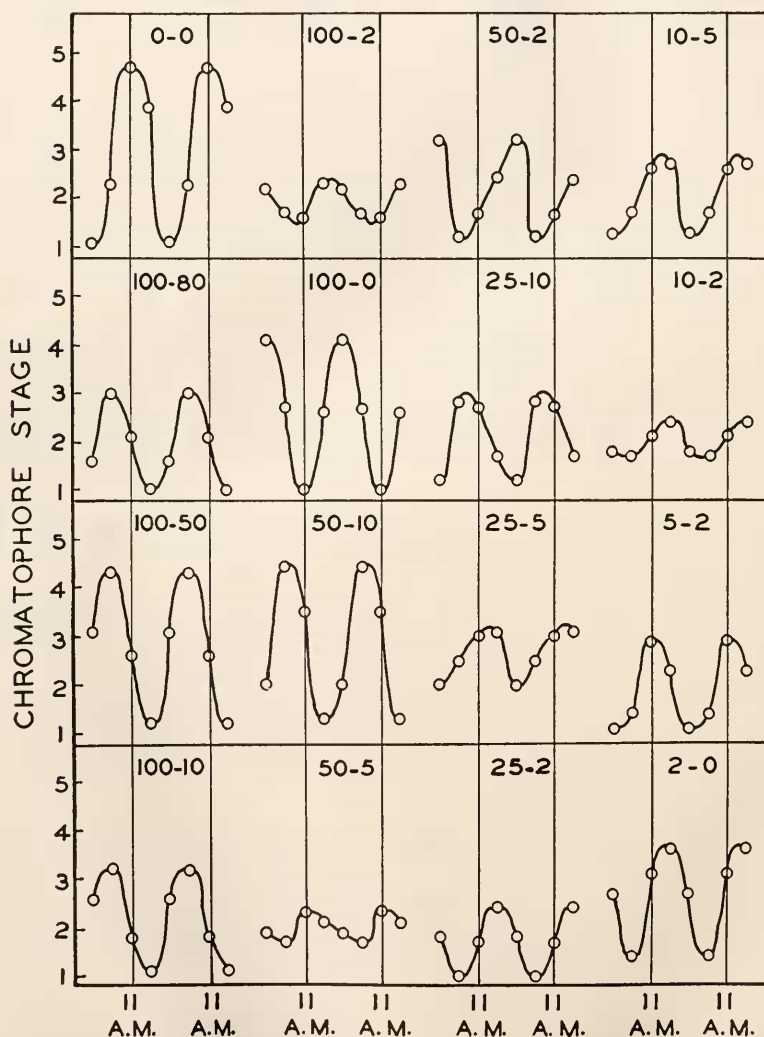

FIGURE 1. The average form and phase relations of the daily melanophore rhythm of *Uca pugnax* in constant darkness after five days of subjection to various higher illuminations by night and lower ones by day. The night-day illumination combinations are indicated for each rhythm.

dition in the controls, it was considered a reasonable procedure to average the values for each time of day for the five days for each group, plot these averages against time of day, and draw smooth curves. This has been done, and two average daily cycles are illustrated in Figure 1. Obviously, the amplitudes illustrated are only the mean ones for the five-day periods, but the forms of the curves and the relationship of the times of their various phases to the actual hour of the day are the factors of chief concern in this consideration. These two factors showed no significant alteration during the five days as is quite evident from Table I.

An examination of Figure 1 clearly shows that the control curve obtained in continued darkness can be illustrated as a more or less sinusoidal one with a

TABLE II

The number of hours by which the phases of the persistent daily rhythm are shifted forward (+) or backward (−) by alternating periods of brighter illumination by night and dimmer illumination by day

Shift of maximum (hrs.)	Illumination night-day (ft. c.)	Shift of minimum (hrs.)	Illumination night-day (ft. c.)
+12	100–0 50–2	+12	100–0
+9	100–2	+9	100–2 50–2
+6	25–2 10–2 2–0	+6	25–2 10–2 2–0
+3	25–5 10–5	+3	50–5
0	50–5 5–2	0	25–5 10–5 5–2
−3	25–10	−3	25–10
−6	100–80 100–50 100–10 50–10	−6	100–80 100–50 100–10 50–10

maximum at 11 A.M. and a minimum at 11 P.M. In sharp contrast with this control, those crabs which had been subjected to 100 ft. c. by night and darkness by day, though similarly capable of depiction as a relatively simple sinusoidal rhythm, were in almost exactly opposite phase.

Although the great majority of the experimental groups appear capable of description in terms of simply a change in amplitude of the cycles, together with more or less displacement forwards or backwards in time relative to the control, there are a few that appear quite definitely to have undergone a modification of form capable of approximate description in terms of the times of maximum and minimum having

been displaced to different extents away from the controls. This is evident in the 50–2 ft. c. group in which the minimum appears to have been displaced to the right by only about 9 hours while the maximum was being shifted by 12 hours.

Comparable differential shifts are also apparent in the 25–5 ft. c. group, where the minimum appears unshifted while the maximum is moved about three hours to the right, in the 10–5 ft. c. group where almost exactly the same situation obtains, and in the 50–5 ft. c. group where the maximum is probably unshifted and the minimum moved to the right, by about three hours.

The differential shifts just described give rise to persistently skewed daily cycles as is evident from all of these curves.

If one considers the 100–0 ft. c. group with a completely reversed rhythm as having both maximum and minimum displaced to the greatest extent, and this to be 12 hours to the right, or forward, in each case, all the other experimental groups tend to fall naturally into a series of lesser amounts of shift to the right, through no shift, and finally to a maximum amount of shift to the left, or backward, of 6 hours. This graded series is described in Table II.

Study of Table II reveals that with 100 ft. c. by night and darkness by day, both maximum and minimum points in the daily cycle are considered as shifted 12 hours forward. For the same illumination by night, an increase in the illumination by day progressively decreases the amount of the shift. With 2 ft. c. by day, the shift is only about 9 hours; with 10 ft. c. by day, the shift is 6 hours backwards, and this value is not exceeded for 50 and 80 ft. c. by day. Similarly for 50 ft. c. by night the greatest amount of shift, 9 to 12 hours forward, occurs when the day value is 2 ft. c. At 5 ft. c. by day the amount of shift has dropped to 0 to 3 hours; and elevating the day to 10 ft. c. produces again the maximum shift backwards of 6 hours.

A comparable series is seen for 25 ft. c. by night. Two ft. c. by day yields a 6-hour shift forwards, 5 ft. c. a 0- to 3-hour shift forwards, and 10 ft. c. a 3-hour shift in the opposite direction. Similarly for 10 ft. c. at night, 2 ft. c. by day gives a 6-hour forward shift, while 5 ft. c. by day yields only a 0-3-hour one.

Five ft. c. by night and two by day produces no change in either direction. Two ft. c. by night and darkness by day gives a 6-hour shift forward.

It is evident that 25 ft. c. at night is not sufficiently great to produce the maximum shift of 6 hours backwards, only 3 being possible. And 10 ft. c. by night appears to be capable of producing no backward shift whatsoever.

These results suggest that for darkness by day, there is a direct relationship between the number of hours of shift and the illumination by night. One-hundred ft. c. gave the maximum shift of 12 hours forwards; two ft. c. gave only about 6 hours forwards. It seems reasonable to postulate that for other values between 100 ft. c. and darkness, other degrees of shift ranging down to no shift at all might be found.

In summary, the amount and direction of shift of the phases of the persistent diurnal rhythm appear to be determined in these experiments by at least two factors. One is the strength of the stimulus in the form of a light increase at 7 P.M., and the other is the intensity of the illumination during the period from 7 P.M. to 7 A.M. A minimum intensity of 50 to 100 ft. c. during the 7 P.M. to 7 A.M. period is necessary to produce the maximum 6-hour shift backwards, and the minimum strength of the stimulus of illumination change at 7 P.M. necessary to produce the

total 12-hour forward shift is produced by some light change between 0–100 or 0–50 ft. c. on the one hand and 2–100 or 2–50 ft. c. on the other.

All of these results, and others that have been obtained in previous work with respect to shift in phases of the diurnal rhythm by illumination changes, are capable of being explained in terms of one hypothesis which will now be presented.

Let it be assumed that the endogenous rhythm in those crabs is one in which the general form of some key aspect of the rhythm can be described as illustrated in Figure 2. Instead of being composed of symmetrical cycles, it is skewed so that one limb is of about 6 hours in duration and the other one about 18 hours. Let the normal relationship of the phases of this endogenous rhythm to the solar day be
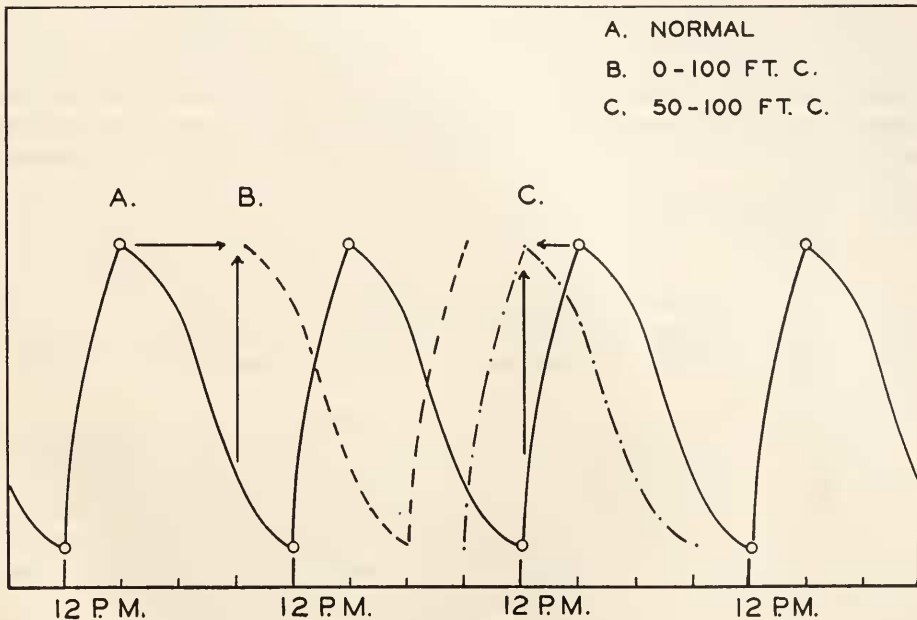

FIGURE 2. Diagram describing an hypothesis for the mechanism of inducing persistent shifts in rhythm phase by light stimuli. Solid curve—normal phase relations. Broken curve —rhythm reversed by a strong illumination change stimulus at 7 P.M. Dot-dash curve—6-hour backward shift by bright illumination from 6 P.M. to 6 A.M. (See text for discussion.)

as indicated in the figure, with the minimum occurring at about midnight and the maximum at about 6 A.M. Since in nature this maximum is normally correlated with the rapid morning increase in illumination and the succeeding 12 hours of the rhythm is normally correlated with the period of daytime, let it be assumed that both of these are normally involved in the bringing of the phases of the endogenous rhythm into their usual and characteristic relationship to the daily light cycle.

In this hypothesis, a strong stimulus in the form of a large increase in illumination at 7 P.M. (*e.g.*, 0 to 100 ft. c. . . .) induces the endogenous state normally correlated with the maximum in the endogenous cycle, or what would amount to a displacement of the phases of the rhythm 12 hours to the right or forward. Smaller

increases in illumination at 7 P.M. (*e.g.,* 2 to 100, 2 to 25, and 5 to 10 ft. c.) would have progressively less effect and the cycle of the endogenous rhythm would be displaced progressively less to the right and only to a degree that the displaced cycle at 7 P.M. was brought into an equilibrium for the light-increase stimulus. To an intensity change represented by the 5 to 50 or 2 to 5 ft. c. shifts at 7 P.M., the endogenous rhythmic mechanism appears normally to be in equilibrium. At still lower strengths of the "shift stimulus," *e.g.,* 10–25 and 10–50, and 10–100 ft. c., the strength can be considered less than the equilibrium one, but now the phases of the rhythm will not automatically shift backwards. The backward shift, if permitted by the intensity-change stimulus strength, is induced by the continuing illumination. A value higher than 25 ft. c. during the 7 P.M. to 7 A.M. period is necessary to move the phases of the rhythm backwards to the maximum extent of 6 hours, the limit being determined possibly by the correlation of the time of minimum strength of the light-shift stimulus at 7 P.M. with the minimum in the endogenous daily rhythm. It seems reasonable to assume that the continuing illumination exerts its backward shifting action at the time of the ascending limbs of the cycle, namely between about midnight and 6 A.M., but that this cannot occur except in the absence of a threshold light change at 7 P.M. Illuminations of 25 ft. c. or below produce less shift, backward, as a direct function of intensity.

An endogenous daily rhythm curve of the kind illustrated in the hypothesis is not entirely without experimental support. This postulated one has almost exactly the same form and phase relations with respect to the day-night cycle as has the rhythm of retinal-pigment movement in the shrimp, Palaemonetes (Webb and Brown, 1953). *Uca pugilator* melanophores in autotomized legs also exhibit a 6-18-hour daily cycle.

In addition to accounting readily for all the results in the current complex series of experiments, it also explains readily the well-known shift of 6 hours backwards obtained by Webb (1950) by three consecutive daily periods of bright illumination from 12 midnight to 6 A.M., and then a few days later still another backward shift of 6 hours to a total of 12 hours, by three consecutive daily periods of illumination from 6 P.M. to 12 midnight. It also provides an explanation for the value, 6 hours, which in much of the initial work on the mechanism of shift of the endogenous rhythm, appeared to come forth with an inexplicably high frequency.

Speculating further upon the actual nature of the physiological processes involved in these light-induced shifts probably would not be very productive at this time. One of numerous possibilities could be that the hypothetical curve describing the diurnal rhythm is a curve describing the intensity of a physiological state which may be altered by light stimuli. A change from darkness to light at any time during the endogenous reduction of this state could elevate it in proportion to the strength of the stimulus. Once abruptly altered in this manner, the endogenous, temperature-independent mechanism could take over with the cycle exhibiting a renewed start at a point in the cycle normally characterized by this higher level. Increase in level of this rhythmic state would be the equivalent, during the descending portion of the curve, to moving the phases of the cycle to the right. On the other hand, the ascending limb of the curve describing an increase in the intensity of the state of the rhythm could be capable of being accelerated by light up to the degree that is nearly instantaneous, provided the phases of the rhythm had not been rigidly de-

termined at an earlier stage in the same cycle by threshold change from light to darkness for that particular phase of the cycle. This would amount to a shift of the phases of the cycle to a maximum of 6 hours to the left. This would not shift further to the left, because the presence of a sub-threshold dark-to-light stimulus for 7 P.M. would earlier in each cycle have freed the cycle to move to a point with the minimum at 7 P.M.

SUMMARY

1. A study was made of the mechanism of reversal of phases of the persistent daily rhythm in the fiddler crab, *Uca pugnax*, by illumination by night and darkness by day.

2. Fiddler crabs were subjected to a series of combinations of brighter illumination by night and dimmer illumination by day.

3. A graded series of amount of shift was obtained which was capable of being interpreted in terms of two operating factors: (a) the strength of the stimulus in the form of the dark to light change, and (b) the absolute brightness of the higher illumination.

4. An hypothesis is advanced which appears to account adequately for all currently known characteristics of the mechanism of persistent shift in phases of the daily rhythm by light stimuli.

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